

On *Cuscuta Gronovii*.

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(WITH PLATE VIII.)

For a parasite that is parasitic from its heart and with all its heart, after having tried an honest life, there is perhaps no better example than dodder, which in our region (S. Hadley, Mass.) is *Cuscuta Gronovii*. We find it in abundance in autumn, early and late, twining its orange-colored stems about grass, solidago, alder, and the like, with a glory of white, bell-shaped flowers, in cymose clusters, appearing as lateral buds in the axils of bracts.

In preparing for the study of *Cuscuta*, fresh plants were placed in alcohol, some were dried—as gathered on the host—and seeds were sowed in pots. From the first, imbedded in celloidin, slides were prepared. The dried specimens yielded knowledge of external parts and abundance of seeds, which were valuable in ways that will appear later. The seeds are exalbuminous, of comparatively large size, with a conspicuous hilum and hard testa; but the latter yielded readily to soaking in dilute potash, and careful dissecting removed the two coats and freed the coiled, snake-like embryo (fig. 1). The root end of the embryo lies outermost, and is slightly enlarged, more noticeably so after germination, when it evidently remains, for some time, a store-house of nourishment.

The time required for germination was found to vary much. Some of the autumn-gathered seeds germinated in three days, after a few days' soaking; others, obtained from alder twigs out of doors, in February, and sowed dry, were three weeks in showing signs of life. The end of the stem which first emerged from the seed-coats was very soon covered with numerous short rhizoids, and careful observations failed to discover any trace of a root-cap. Figs. 2 and 3 illustrate seedling dodders. The tip produces, even at a very early stage, the rhizoids mentioned. Comparing fig. 3 with fig. 1, it will be seen that the root-hairs must have grown very rapidly, none being on the embryo, just before germination. Fig. 2 is the root end of a seedling 2 inches long, and hence the rhizoids are much further developed. Fig. 5 illustrates one of the most interesting things in my study of the plant, and one that I could not find mentioned by any

observer, viz., a method by which the plant cut itself off from normal nutrition. Having reached some suitable host—a twig of *Forsythia viridissima* in this case—it twines around it like a tendril, by two or three coils, and in coiling contracts so as to draw itself nearer the host. This contraction, if the seedling is not too deeply rooted, or too slack between the soil and the support, pulls the roots from the earth and leaves the plant—a parasite by suicide—with roots at varying distances above the soil, $\frac{1}{4}$ of an inch being perhaps the highest I observed. If the plant is not uprooted in this manner or by the lengthening of the internode of the host to which it is attached, as sometimes happens, the lower part of the stem dies, and the connection is thus severed with the absorbing root, not, however, until the enlarged portion of the stem has been drained of its nourishment or the plant has reached some other supply. All the plants that germinated earliest, of those we studied, hung themselves; the later ones—those washed deeper into the soil—died at base. Our gardener, noticing the hanging ones, said, “Those are not plants; they crawl up sticks like an inch-worm.” These germinating plants are white below, but yellowish-green at summit, suggesting that the dodder, even in its degeneracy, has some chlorophyll and may elaborate food for a short time. The amount of nourishment stored in the embryo hardly seems sufficient to enable the seedling to produce such a length of stem before reaching a host, as is done by some. Other things, too, indicate ability to assimilate, such as the greenness of buds and branches for some time after they appear. This coloring matter is removed by alcohol.

To illustrate the rapidity of growth after germination, I give the statistics of a single plant, grown in my own room under a bell-jar, in circumstances perhaps not the most favorable, as there was much variation in temperature, especially at night. The seeds were collected out of doors on some alder twigs, and sowed immediately, February 29. The first plantlet appeared at the surface of the soil March 20, and twenty-four hours later, at 8 A. M., March 21, was one inch long, with tip doubled back and coiled once about itself like a whip upon its stalk. All was white but the coiled tip. At 10 A. M. it had more nearly uncoiled and had gained one-fourth inch in length in the two hours; at twelve it was erect and slightly elongated; at 6 P. M. its length was one and one-half inches and its inclination toward the nearest host. Measurement at 8 A. M., March 22, showed it to have

gained three-fourths of an inch in twenty-four hours—one-third of that length between 8 and 10 A. M. Careful observation between the corresponding hours the second day showed the same gain, suggesting, what experiments with other seedlings seemed to corroborate, that 8 to 10 A. M. represented the maximum period of growth. The plantlet was then, at the height of two inches, touching its host. Contact caused it to coil like a tendril, although it was several times disturbed and shaken from its support, so that at 8 A. M., Saturday, the 24th, three days after germination, it was fast to its host with two close coils about the stem. Growth in length now ceased for several days, all its energy being expended in producing suckers and thrusting the haustoria into the host. March 26 the suckers were well developed, the root portion was brown and useless, the reservoir above the rhizoid portion exhausted of supplies and the plant apparently in position for an easy life. During this time the nutation of the tip of the seedling was opposite to the course of the sun.

From observation upon this and other plants it was evident that there is a limit to the size of stem they are able to encircle, and that the diameter must be small. One that I noticed attempting to surround a large geranium stem was unequal to the task, and coiled back upon itself twice upon the side of the trunk. Plants showed very little discrimination in the selection of hosts, attacking everything that offered support—dead and dying stems, as well as fresh ones, and even the rim of the flower-pot. They usually recoiled after one turn about a dead twig, and extended the tip further unless the root had been lifted from the soil. When a suitable host was obtained, the tip nestled down close to it and did not attempt further wandering.

We failed, for a long time, in all our attempts to cultivate the dodder—further than to obtain a few coils about the stem. We never suspected the unsuitable character of the hosts, as out-door dodders do not seem particular. But an enterprising seedling taught us the lesson by seizing a young geranium petiole, just emerging from the bud, and beginning to grow by feet in the same pot where a *Eupatorium*-entertained companion, of the same age, grew scaly, stubby and by inches, and all others died. After this there was no difficulty in raising dodders.

The suckers are, outwardly, enlarged fleshy disks, which the parasite forms and presses hard against the host, sending

into it from their center organs called haustoria by which they absorb the elaborated juices as roots take moisture from the soil. They differ from true roots, as does the root-acting end of the stem, in the absence of a root-cap.

An attempt to remove the dodder from a stem to which it is well attached often ends in taking with it at least the cortex of the plant on which it grows. Sections either longitudinal or vertical through the parasite, in position on its host, median as regards a sucker, will explain this. Each sucker starts, as does a root, in the vascular tissue of the stem, and is a cylinder, sharpened like a blunt pencil where it enters the host and enlarges immediately afterward. Thus is made a sort of neck about which the epidermis of both host and parasite fit very neatly; the sudden enlargement of the latter, in its new quarters, serving, as does a nut on a bolt, to prevent its easy removal.

The suckers, in their origin, are domes of meristem tissue before they reach the epidermis. Whatever lack of discernment the dodder may show in its selection of a host, once well placed, it lives up to its opportunities. It may, and usually does, in a woody stem like that of *Solidago*, send one root into the center, as if for deep anchorage, but spreads out by far the larger portion of its absorbing tissue in the cambium and sieve-tube regions where elaborated material is most abundant. Its tissue is easily distinguished from that of the host by its enlarged thin-walled cells with prominent nuclei. When the cutting was exactly median, the tissue seemed like a compact cylinder made up of filaments of cells, end to end, like meristem tissue, which branched, however, in a variety of ways inside the host. When growing on hollow stems like grasses, as it was common to find them, the haustorium scarcely branched, there being little opportunity.

One of the most singular phases of dodder life was a sort of self-grafting or self-parasitism. With a low power it was difficult to distinguish which was host and which guest, as the haustorium extended from the vascular region of one stem to the same of another. In examining the alcoholic specimens, I found this common, and it has often been repeated on those growing in my own room, usually under such circumstances as these: If a parasite had occasion to twine about an already thickly covered host, in its anxiety to obtain its share of elaborated material, it was willing to take a sort of second mortgage upon it, after it had passed into

the tissues of the first; this inter-parasitism also occurs frequently when for a long distance stems intertwine.

There is little differentiation in the tissues of the dodder; it needs, very early, conducting tissue for carrying moisture through the stem to the rapidly growing and probably assimilating apex. To meet this need vascular tissue is found as soon as germination takes place. It is very simple, consisting of alternate stripes of tracheids and parenchyma, each about two rows of cells broad, and in the best developed stems occupies perhaps from one-third to one-half the diameter. It is well adapted for twining by this alternation with the softer parts, while the predominance of the latter favors the carrying of elaborated material, as it is in these such products travel. Iodine testifies to the presence of starch in the tissues of mature plants. Other reagents show, as do the markings on the walls, the woody nature of the alternate bands evident in a section of stem.

Of the adventitious buds, known to be abundant in the dodders, I have studied only those producing branches.

Their origin was in this manner: When a parasitic root had become well established, so that the plant was thoroughly engrafted upon the host, in an axil thus formed, a branch would arise, after the manner of an axillary branch on a normal plant. The regular branching of a stem of *Cuscuta* is unusual in the centrifugally arranged accessory buds (figs. 6 and 7), the last formed bud being farthest from the parent stem, though sections show it to originate in the axil bundle.

The epidermis of dodder varies with its position. On the long internodes between adjacent scales stomata are rare, while over suckers, *i. e.*, on the side of the stem opposite them, very small stomata are quite abundant. This explains, in a measure, the continuance of life and growth for two weeks or more in branches cut from the parent stem and suspended in the air, though such stems never form coils or suckers.

Each flower has a short pedicel like the main stem in structure, a thickened receptacle, a five-lobed calyx and corolla with beautifully branched fringes lining the latter, and adherent stamens alternating with its lobes; the ovary has two cells with two ovules in a cell, and there are two knob-like stigmas on short styles. As to the manner of fertilization of the dodder, whether self or cross fertilized, I have had no opportunity to observe.

The two-celled ovary is composed of two carpellary leaves, with two cushion-like basal placentæ, each bearing two ovules, though at maturity there is often but one. The sections of placentæ are deceptive when the ovules are absent, having much the appearance of young ovules. The study of the ovules with reference to the layers in the seed coat gives evidence that in the mature testa there are three. The outer is quite unlike the two below, which are, perhaps, divisions of the same cell layer. They probably arise and cover the nucellus in an early stage, but are not differentiated into the mature form until a late period in the maturity of the ovule.

A short distance below the apex of each mature embryo, and always on the inside of the curve, as it lies coiled in the seed, is a well-developed scale (figs. 8 and 9, *a*). Another scale almost as well developed is usually to be found slightly below the apex of the embryo, but on the outer side of the curve (figs. 8 and 9, *b*). These two are separated by quite a portion of the stem in length, and in some cases the second scale is only partially differentiated, and yet a part of the tip, whose tissues, under a high power, are evidently of scales in process of formation. In no case were the scales opposite, or approximating it, as a pair of cotyledons would stand. What may be their relation to the embryo, I do not know, but the apex with its forming scales, of which this second one is sometimes a part, could well be a plumule. Comparing seedlings two inches in height with the embryos, the scales were evident (at least always the inner one), and at a distance from the growing tip corresponding to the increased length of the plant. They in every case soon turned brown.

How the dodder became a parasite is an interesting theme, and pleasantly treated in an article in the *Popular Science Monthly*, Vol. XXV. A weak stem, desire to reach the light, twining to accomplish this, and tasting juices by chance, they were nourished by them and given a tendency which increased in favorably situated descendants until, as Drummond states: "Henceforth to the botanist the adult dodder presents the degraded spectacle of a plant without a root, without a twig, without a leaf, and having a stem so useless as to be inadequate to bear its own weight." So it stands a monument of degeneration. Other plants with smaller beginnings have gone on to higher forms, while the dodder, as Prof. Drummond again, in substance, says, from

a breach of the laws of evolution, pays one of Nature's heaviest fines—loses the organs it once had.

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EXPLANATION OF PLATE VIII.—Fig. 1, mature embryo, dissected from seed. Fig. 2, tip of root of *a*, fig. 5. Fig. 3, enlarged view of 4, an embryo one-half nat. size, just escaped from seed coats. Fig. 5, seedlings, one-half nat. size. Figs. 6 and 7, accessory branching. Figs. 8 and 9, tips of embryos, enlarged; *a*, inner, lower scale; *b*, outer scale.

Development of cork-wings on certain trees. V.

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Passing now from stems of this type to those of *Liquidambar*, it is readily seen that whatever may be the end results, the immediate causes producing the wing are not the same as in the former type. Its eccentric development is a marked peculiarity, which, so far as I have been able to discover, occurs in no other instance. The question at once arises, whether the causes which produce eccentricity of growth in the annual rings of wood are likely to extend to the tissues arising from the cork cambium. If this were proven to be the case it might help but little in solving the problem before us, as it is a well known fact that the best authorities do not agree as to the causes of eccentric growth in woody tissues.

The function of protection which is universally assigned to the periderm naturally requires greater flexibility of structure, varying degrees of thickness, greater or less permeability for water and gases according to varying outward conditions, and, finally, greater or less outlay of material, which, in some cases, is retained, in others, discarded by the plant after it has performed its function. In this way it is easy to account for the variableness in periderm formation as illustrated in the genus *Euonymus*. This is more striking when contrasted with the uniformity prevailing in the structure of woody tissue. For example, when examining a large number of woods in regard to the presence or absence of bordered pores in the libriform, it was found quite unnecessary to carry the study farther than the genus. If a single species contained libriform with bordered pores, this was sufficient for the genus.